Genetic Diversity and Geographic Differentiation in Quantitative Traits, and Seed Transfer Guidelines for Whitebark Pine

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Whitebark pine (*Pinus albicaulis* Englem.) has declined dramatically throughout its range due to white pine blister rust (caused by the fungus *Cronartium ribicola* J.C. Fisch.), successional replacement resulting from fire suppression, and attack by mountain pine beetle (*Dedroctonus ponderosae* Hopkins). Restoration is needed to halt or reverse this decline; however, no information regarding genetic diversity and local adaptation of quantitative traits is available to guide these efforts.

A seedling common garden experiment was employed to assess genetic diversity and geographic differentiation of quantitative traits (Q_{ST}) of whitebark pine and to determine the climatic variables driving local adaptation. Seedlings from 48 provenances from a near range-wide seed collection were grown in raised beds in Vancouver, B.C. for two years in two soil temperature treatments (ambient and cold). Seedlings were measured for second year height increment, total biomass, root:shoot ratio, date of needle flush, fall and spring cold injury, and survival.

Significant differences were found between soil temperature treatments for height growth and survival, with seedlings in the cold treatment performing better. The environment where the test was grown (Vancouver, B.C.) is considerably warmer than the natural habitat of whitebark pine. While most temperate forest trees would likely benefit from the warmer soil temperatures, it appears that this is a stressor for a species adapted to cold, harsh environments.

We observed significant differences among provenance means in most quantitative traits (Table 1), similar to many other widespread North American conifers. Differences among provenances accounted for a substantial proportion of the variance only for cold acclimation traits (date of needle flush and fall cold injury), indicating that provenances are under stronger differential selection for these traits than for growth. In the common garden environment, provenances from higher latitudes and lower winter temperatures flushed earlier in the spring, suffered less cold injury in the fall, and allocated more biomass to shoots. In the subalpine environments where whitebark pine grows, these traits most likely have a larger role than growth traits in determining local fitness and the ability to withstand abiotic stresses associated with local climate.

Table 1. Significance level of provenance effect in ANOVA, proportion of variation accounted for by provenance and family, and genetic differentiation (Q_{ST}) for nine quantitative traits in ambient (A) soil temperature treatment and seven traits in cold (C) treatment.

Variable	**Provenance**		σ^2_P/σ^2_T	σ^2_F/σ^2_T	Q_{ST}
	F-value	**p-value**			
A-Height increment[ab]	1.84	**0.01**	0.05	0.05	0.14
A-Total dry mass[ab]	1.69	**0.01**	0.04	0.09	0.07
A-Root dry mass[ab]	1.65	**0.02**	0.03	0.07	0.08
A-Shoot dry mass[ab]	1.73	**0.01**	0.04	0.10	0.07
A-Root:shoot[ab]	1.09	0.35	0.00	0.03	0.00
A-Date of needle flush 2003[a]	6.51	**<0.001**	0.26	0.05	0.47
A-Date of needle flush 2004[a]	5.49	**<0.001**	0.23	0.04	0.47
A-Fall cold injury	2.59	**<0.001**	0.19	0.06	0.36
A-Spring cold injury	1.11	0.33	0.05	0.07	0.12
C-Height increment[b]	1.57	**0.04**	0.07	0.07	0.13
C-Total dry mass[b]	1.24	0.20	0.06	0.11	0.09
C-Root dry mass[b]	1.22	0.22	0.05	0.10	0.08
C-Shoot dry mass[b]	1.23	0.21	0.06	0.11	0.08
C-Root:shoot[b]	1.09	0.36	0.01	0.08	0.01
C-Date of needle flush 2003	3.29	**<0.001**	0.21	0.05	0.43
C-Date of needle flush 2004	6.36	**<0.001**	0.33	0.03	0.65

[a] A=ambient soil temperature treatment, C=cold soil temperature treatment
[b] Natural log transformed

Genetic differentiation (Q_{ST}) was moderate for growth traits (height increment and biomass) and strong for cold adaptation traits (date of needle flush and fall cold injury). For all traits Q_{ST} was greater than previously published estimates for whitebark pine based on range wide studies using molecular markers (F_{ST}) (0.034-0.046), indicating natural selection driving local adaptation.

Canonical correlation analysis was used to examine the relationship of quantitative traits with climatic and geographic variables, and to determine whether variation in quantitative traits among provenances is clinal. The results of this analysis were then used to develop predictive equations for the construction of seed transfer guidelines. Values of significant canonical variables associated with the quantitative traits were regressed on the standardized key climatic variable with the highest loading for that canonical variable. The slope of this regression provides a rate of change in the canonical variable associated with the quantitative traits relative to the climatic variable. Rates of differentiation along climatic gradients were interpreted relative to the least significant difference among provenances at the 20% level (LSD 0.2). This reduces Type II error - accepting no differences among provenances when differences actually exist. The rate of differentiation of the key quantitative traits associated with canonical vectors was determined as the change in the standardized climate variable associated with the LSD value of the canonical variable. The difference in the climate variable associated with significant genetic differentiation between provenances was calculated as the rate of differentiation multiplied by the standard deviation of the climate variable.

The first pair of canonical variables demonstrates the effects of mean temperature of the coldest month. The positive correlations of date of needle flush and fall cold injury with the first canonical variable (Figure 1) indicates that trees from provenances with higher mean temperature of the coldest month flush later in the spring and suffer higher cold injury in the fall. The second pair of variables demonstrates the effect of the length of the growing season (FFP), with trees from provenances with longer growing seasons growing taller, and producing more biomass.

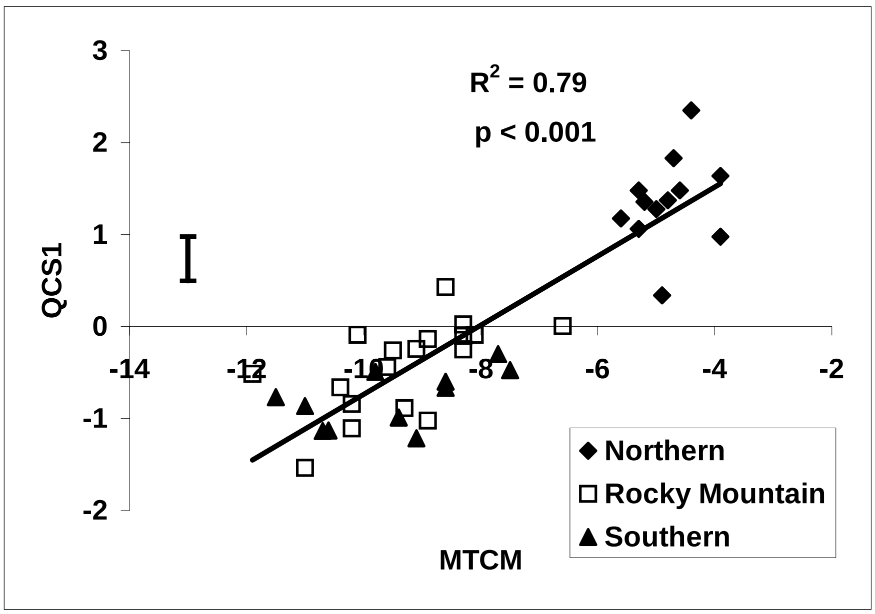

Figure 1. Regression of first quantitative canonical score (QS1) on standardized mean temperature of the coldest month (MTCM) for 41 whitebark pine provenances in three geographic regions. Axes scales are standard deviations and bracket indicates value of LSD 0.20.

Cold adaptation traits were strongly influenced by mean temperature of the coldest month, while growth traits were influenced by the length of the growing season. Guidelines for seed transfer in restoration programs based on these results indicate that whitebark pine seed can be moved within areas differing by 1.16^o in mean temperature of the coldest month or approximately 3^o in latitude with minimal risk of maladaptation. The difference in elevation required to distinguish genetically different populations (~700m) exceeds the elevational range of whitebark pine within 3^o of latitude, so there should be no elevational restrictions on seed movement.

The role of climate change in the future of whitebark pine is uncertain, and restricting movement of seed to the south may provide a buffer against future climate warming. Therefore, movement of whitebark pine seed should be restricted to 3^o to the north and less than 1^o to the south in order to minimize maladaptation in current and future environments. The predicted increases in temperature will push whitebark pine beyond the geographic limits to which is locally adapted and will likely result in a dramatic reduction in suitable habitat, potentially decreasing genetic diversity. Damage and mortality due to blister rust is a primary concern for whitebark pine; however, the potential affects of climate change should not be underestimated. Without restoration and conservation efforts using appropriate seed sources that will be adapted to new climatic conditions, the decline of whitebark pine is likely to be accelerated, with the potential of extirpation in some areas. The data and results presented here are crucial for restoration efforts that will be necessary to maintain whitebark pine as more than a minor component of the ecosystems in which it plays such a vital role.